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Systematics and evolution in the savanna species of the genus *Batis* (Aves) in Africa

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Abstract. A systematic review of the populations of the savanna species of the African flycatcher genus *Batis* is given with descriptions of the geographical variation exhibited by the populations. An analysis of the variation in colouration and size is presented using nonmetric multi-dimensional scaling technique to present a three-dimensional plot of the relationships of the populations as determined by their phenotypic variation, as well as a dendrogram of the relationships of the populations using the Unweighted Pair-group Method using Arithmetic Averages. Observations on the possible evolutionary history of the species are given.

Key words. Aves, Platysteiridae, Batis, systematics, evolutionary history, Africa.

Introduction

The avian flycatcher genus *Batis* is confined in its distribution to subsaharan Africa. The eighteen species comprising the genus can be sensibly divided into two groups, those that inhabit forests and those whose preferred habitat type is woodland savanna. The systematics and speciation of the forest-dwelling species has been the subject of a study (Lawson 1986). This paper reports on a study of the savanna-dwelling species of *Batis*.

The eighteen species of *Batis* are *capensis*, *mixta*, *reichenowi*, *margaritae*, *diops*, *minima*, *ituriensis*, *fratrum*, *minulla*, *occulta* and *poensis*, the forest species, and *molitor,pririt*, *soror*, *orientalis*, *minor*, *perkeo* and *senegalensis*, the savanna species. The only feature of plumage colouration which distinguishes the forest from the savanna species in the colour of the under wing coverts, which are white in the forest species and black in the savanna species. It is interesting to speculate whether the under wing coverts and their colour play any part in signalling in courtship or mating behaviour of *Batis* individuals, as this colouration difference may have been important in the original speciation or splitting of the *Batis* populations into forest and savanna species. A signalling difference of this kind between mating partners could have been significant in the Specific-Mate Recognition System (A discussion of the Specific-Mate Recognition System is given by Paterson 1985).

Materials and methods

Material. Study skins for this project were obtained on loan from museums in Africa, Europe, Australia and the United States of America. For the loan of study material I am indebted to the Directors and responsible officials of the following Institutions:

Angola: Instituto de Investigacao Cientifica de Angola, Sa da Bandeira. Museu do Dundo, Dundo. Australia: Australian Museum, Sydney. Belgium: Musee Royal de l'Afrique Centrale, Tervuren. Federal Republic of Germany: Zoologisches Museum Alexander Koenig, Bonn. France: Museum d'Histoire Naturelle, Paris. German Democratic Republic: Institut für Spezielle Zoologie und Zoologisches Museum der Humboldt Universität, Berlin. Kenya: National Museum, Nairobi. Moçambique: Museu Dr Alvaro de Castro, Maputo.

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Namibia: State Museum, Windhoek. Netherlands: Rijksmuseum van Natuurlijke Historie, Leiden. South Africa: Albany Museum, Grahamstown, Durban Natural History Museum, Durban, East London Museum, East London, Kaffrarian Museum, King William's Town, Natal Museum, Pietermaritzburg, Port Elizabeth Museum, Port Elizabeth, South African Museum, Cape Town, Transvaal Museum, Pretoria. Sweden: Naturhistoriska Riksmuseet, Stockholm. United Kingdom: British Museum of Natural History, Tring. United States of America: American Museum of Natural History, New York, Carnegie Museum, Pittsburgh, Field Museum of Natural History, Chicago, Los Angeles County Museum, Los Angeles, Museum of Comparative Zoology, Cambridge, Peabody Museum of Natural History, New Haven, Philadelphia Academy of Natural Sciences. Philadelphia, United States National Museum, Washington. Zambia: Livingstone Museum, Livingstone. Zimbabwe: National Museum of Zimbabwe, Bulawayo, Queen Victoria Museum, Harare.

Table 1: Characters of savanna-dwelling Batis used in MDS and UPGMA analysis.

	O' O'	Q Q
1	mantle colour	mantle colour
2	head top colour	head top colour
3	flanks colour	flanks colour
4	breast-band colour	breast-band colour
5	throat-patch colour	throat-patch colour
6	tertials colour	tertials colour
7	primary coverts colour	primary coverts colour
8	lores colour	lores colour
9	supra-loral spot	supra-loral spot
10	supercilium colour	supercilium colour
11	under-wing coverts colour	under-wing coverts colour
12	mean wing length	mean wing length
13	mean tail length	mean tail length
14	mean culmen length	mean culmen length
15	_	scapulars colour
16	_	primaries colour
17		secondaries colour
18	_	lesser coverts colour

Methods. Measurements, to the nearest 0.5 mm were taken of the wing, tail and culmen of study skins of adult specimens that were not moulting, badly-worn or damaged. Only measurements taken during the course of this study were used. A number of colouration characters were also recorded (listed in Table 1) for each of which the range of variation was ranked on a scale of 1 to 15. For characters where presence or absence or state of development was important such as the supraloral spot, absence of the character was scored as 1 and the presence of a well developed white supraloral spot was coded as 15; intermediate scores were assigned to varying degrees of prominence. The assessment was subjective. This type of coding was also applied to the width of white edges of primary coverts, tertials and other feathers. For parts of the plumage such as the head top or mantle where a gradation from one colour to another was evident, dark blackish olive brown could be scored 1, and the extreme, a very dark grey heavily suffused with glossy blue-black, as 15. The varying shades of brown to greys with admixtures of blue-black were coded according to where they were perceived to fall in the range of variation. The colours of the various characters were recorded and graded without reference to the populations exhibiting them, thus reducing bias in the ordination of data.

The smallest and largest of the means of the measurements taken for the three mensural characters were ranked 1 and 15 respectively. The differences between them were equally divided to allow ranking of intermediate means. Using the scores allocated to the character states for each population considered, males and females, a 17 x 17 square matrix of disparities was calculated by comparing each population with every other population, and for each pair of

populations a number was calculated as the sum of their absolute score differences for each character. The disparities matrix is symmetrical about the diagonal, so the lower triangular matrix was used as the input data for the non-metric multidimensional scaling (MDS) analysis of the populations (see Figure 1 for the three dimensional plot), as well as for the phenetic dendrogram (Figure 2) constructed using the Unweighted Pair-group Method using Arithmetic Averages (UPGMA). The disparities matrix is given in Table 2.

Table 2: Matrix of disparities of sum of score difference for each character.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
2	47															
3	61	64														
4	56	51	56													
5	67	71	49	47												
6	144	127	155	128	155											
7	148	140	160	139	161	90										
8	139	121	149	127	151	72	46									
9	174	177	158	156	159	146	201	193								
10	146	156	137	142	139	145	197	186	52							
11	131	140	129	138	129	178	207	195	94	67						
12	117	131	137	135	147	172	201	190	111	85	53					
13	140	134	151	123	150	121	167	155	70	61	86	80				
14	133	136	151	129	154	143	185	173	87	59	67	59	40			
15	142	136	152	127	152	122	165	157	75	66	88	84	40	56		
16	209	187	214	188	216	115	161	160	121	138	171	167	118	135	119	
17	275	256	293	271	294	208	237	238	246	221	232	224	209	201	212	202

For the multidimensional scaling analysis the ALSCAL-4 package was used here (see Takane, Young & de Leeuw 1977), as improved by Young, Takane and Lewyckyj (1978), because it consolidates most of the important developments in multidimensional scaling into a single program. These programs begin with an arbitary configuration of points representing the populations and use iteration procedures from this map to improve the fit of the distances between the points to the original disparities. For the use of this method in the forest dwelling species of *Batis* see Lawson (1986) and for a more detailed discussion of the application of the MDS techniques to *Batis* data see Lawson & Stabler (submitted to South African Journal of Zoology).

Results and discussion

Specific limits of *Batis*

While there is little controversy concerning the specific limits of the savanna species of *Batis*, this is not so for subspecific limits. For the seven species of savanna *Batis* I admit as valid some seventeen population groupings as subspecies. In all twenty-six names have been proposed for subspecies of savanna species, most of the nine not accepted as valid here are not admitted as valid by most previous workers on African birds.

Key to the savanna species of *Batis*

1.	females with breast band clearly defined and brown	2
	females with indistinct ochraceous breast band	B. pririt
2.	females with the throat entirely white	3
	females with the throat brown, entirely or in part	4
3.	male mantle grey	B. orientalis
	male mantle grey with blue-black suffusion	B. minor

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4.	females with indistinct throat spot	5
	females with distinct throat spot	B. molitor
5.	females with diffuse brown throat	6
	females with only sides of throat brown	B. perkeo
6.	males mantle grey	B. soror
	males mantle olive russet	B. senegalensis

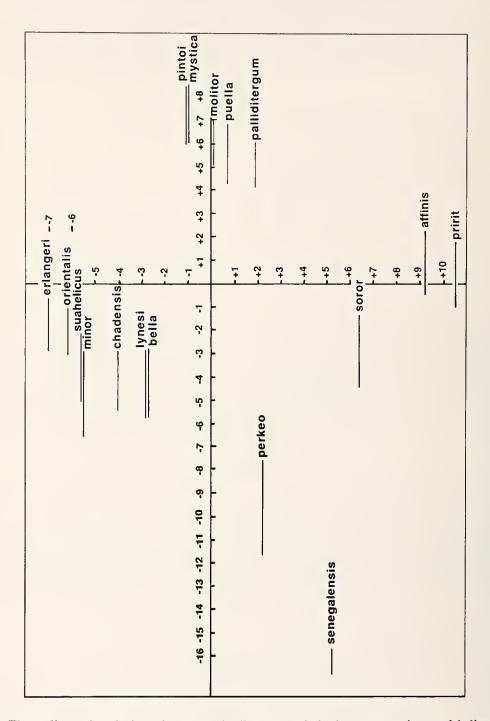


Fig. 1: Three dimensional plot of taxonomic distances of all characters using multi-dimensional scaling technique.

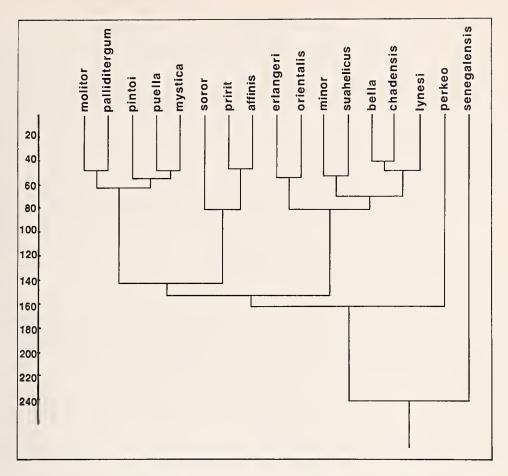


Fig. 2: Phenogram constructed using U. P. G. M. A. to show phenetic relationships of savanna species of *Batis*.

List of savanna dwelling species

The seven savanna dwelling species and their subspecies admitted in this work are

Batis molitor molitor (Hahn & Küster)

Batis molitor palliditergum Clancey

Batis molitor pintoi Lawson

Batis molitor puella Reichenow

Batis molitor mystica Neumann

Batis soror Reichenow

Batis pririt pririt (Vieillot)

Batis pririt affinis (Wahlberg)

Batis perkeo Neumann

Batis senegalensis (Linnaeus)

Batis minor minor Erlanger

Batis minor suahelicus Neumann

Batis minor erlangeri Neumann

Batis orientalis orientalis (Heuglin)

Batis orientalis bella (Elliot)

Batis orientalis chadensis Alexander

Batis orientalis lynesi Grant & Mackworth-Praed.

Species accounts

Batis molitor (Hahn & Küster)

Habitat: *Batis molitor* is an inhabitant of the woodland savannas. The particular botanical association in which it is to be found varies somewhat in the different parts of its rather extensive range (Figure 3). Its range follows closely the distribution of the following vegetational types, grouped as woodland by the *Vegetation Map of Africa* (1958).

type 16 undifferentiated: relatively moist types

- 18 south-eastern areas: with abundant Brachystegia and Julbernardia
- 19 south-western areas (principally on Kalahari sand): with abundant *Brachystegia*, *Julbernardia*, *Cryptosepalum pseudotaxus*, *Marquesia*, *Guibourtia coleosperma*
- 20 undifferentiated: relatively dry types
- 22 with abundat Colophospermun mopane.

Geographic variation: *Batis molitor* has five subspecies which are here admitted as valid. Variation is usually evident in differences in size and colouration of the head top and the mantle. The chestnut breast band of the female is also variable but this variability has not been used as a taxonomic character as it was found that it was not possible to delimit any particular colour variant satisfactorily to any definite geographical area.

Males have the head top and mantle grey, varying from light grey to dark grey with a variable suffusion of glossy blue-black, from absent to heavy. The lores are white which may extend in the form of a very thin white supercilium, extending as far as a position above the eye. The white supercilium may be absent however. The breast band is glossy blue-black, somewhat variable in width. The primaries may or may not have a narrow edge of white on the outer web, the secondaries always have a broad white edge to the outer web.

Females have the head top and mantle grey, varying from light to dark. The breast band is russet, varying somewhat in intensity. A distinct spot of russet on the throat is separated from the breast band by a broad band of white. Other features of the plumage are similar to those of the male.

The subdivision of *B. molitor* into subspecies has been the subject of many divergences of opinion by workers on African birds. Sclater (1930) admitted as valid the subspecies *B. m. molitor*, *B. m. puella* and *B. m. soror*, keeping *B. m. mystica* as a distinct species while placing *B. soror* as a subspecies of *B. molitor*. Chapin (1953) admitted *molitor*, *puella*, *taruensis* and *soror* as subspecies of *B. molitor*. Mackworth-Praed & Grant (1955 & 1963) admit only *molitor* and *soror* as subspecies of *B. molitor*. Similarly White (1963) admits only *molitor* and *soror* but keeps them as separate monotypic species. Clancey (1966) dealing with the southern African populations admits *molitor*, *palliditergum* and *soror* as distinct subspecies in the southern part of the range of *B. molitor*.

In examining samples from the various populations of *B. molitor* from different parts of the species' range, considerable difficulty is encountered in allocating names to the varying populations, and in defining their ranges. White (1963) stated ,,There is so much disagreement as to the recognition of subspecies and their ranges that I

prefer a binomial whilst admitting the existance of varying populations". In this study the colouration of the head top and mantle of males and to a lesser extent of the females, is used as the distinguishing criteria between the admitted subspecies.

The populations of *B. molitor* are continuous and none appear to be isolates. This results in an uninterrupted gene flow through the range of the species and results in poorly defined subspecies in most instances. This variability is precisely what would be expected under these circumstances. The populations of *B. molitor* in areas of contact between the different subspecies in areas with no natural topographic features which could partially inhibit gene flow cannot satisfactorily be pigeon-holed into neatly defined subspecies. There is however evidence that the different subspecies have different ecological preferences, which are elucidated in the descriptions of the subspecies which follows.

B. m. molitor has the upperparts a fairly dark grey whereas B. m. palliditergum is a group of populations which have the head top and mantle a considerably paler grey. Nominate molitor occurs from the eastern Cape Province northwards to the Limpopo River in southern Moçambique and west of the Lebombo Mountains to the low-lands of Swaziland and the eastern Transvaal (only marginally in the latter). The wood-land savanna type inhabited by the nominate race is termed "undifferentiated: — relatively moist types" on the Vegetation Map of Africa (1958). The populations of molitor meet those of palliditergum in the lowlands of Swaziland and the eastern Transvaal and the adjacent areas of Moçambique, south of the Limpopo River. The differences in the colouration of the upper parts constitute the principal difference between the two subspecies.

In the original description of the subspecies *palliditergum* this subspecies was stated to range "From Natal and Pondoland in the south (slightly intermediate), Zululand, Swaziland, extreme southern Portuguese East Africa, the Transvaal, Bechuanaland, ?Damaraland and Southern Rhodesia northwards to parts of Northern Rhodesia, ?western Nyasaland, and apparently the Marungu highland, Belgian Congo, and areas about Lake Tanganyika." (Clancey 1955). However Lawson (1963) amended this range when he extended the range of *molitor molitor* to the eastern Cape Province through Natal, Zululand and southern Swaziland to southern Moçambique, south of the Limpopo River, the range also given by Clancey (1966, 1980).

The populations placed as *B. m. palliditergum* are by no means constant in their characters, although the characters by which they are distinguished from other subspecies are constant. They are all pale mantled when compared with the nominate race and the western *B. m. pintoi* and the northern *B. m. puella* and *B. m. mystica*. The degree of paleness varies from area to area.

The ecological preference of *B. m. palliditergum* follows very closely the ranges given in the *Vegetation Map of Africa* (1958) types 20 & 22 in southern Africa, these being the undifferentiated dry types of woodland and the *Colophospermum mopane* woodland, and in type 18, woodland with abundant *Brachystegia* and *Julbernardia* of Zimbabwe and Zambia east of the Luangwa River, and also in Malawi.

Populations of *B. molitor* in Angola and Kenya have been long placed as *B. m. puella* on the basis of the mantle being heavily suffused with black. Chapin (1953) gave the range of *puella* as "central and northern Angola across the south eastern Congo to Ruwenzori, the interior of Kenya Colony and Kilimanjaro." White (1963)

though not admitting *puella* as a valid race nevertheless admitted the existance of dark backed populations in these areas. However this study has shown that the name *puella* based on material collected at Bussissi on the southern shore of Lake Victoria is not applicable to these dark mantled populations, which are in any event not continuous and are separated into two distinct population groupings, each requiring a separate name.

The populations assigned here to *B. m. puella* have an ecological preference for the *Brachystegia* woodlands, types 18 & 19 of the *Vegetation Map of Africa*, (1958) and occupy almost the entire range of this vegetation type with the exception of the extreme west in Angola where *B. m. pintoi* occurs and in the extreme south and east where *B. m. palliditergum* occurs. To the west of Lake Victoria it also occupies the undifferentiated moist type woodland (type 16).

The populations of Angola, except in the extreme south and north-east, and in north-western Zambia, are a dark grey on the upper parts with a heavy suffusion of black, differing from the pale mantled *palliditergum* and the populations I now place as *puella*, which are also paler on the upper parts. These Angolan populations have been placed as *B. m. pintoi*. This subspecies has an ecological preference for the moist undifferentiated type of woodland, type 16 of the *Vegetation Map of Africa* (1958) in Angola, and also in the extreme western parts of types 18 & 19, *Brachystegia* woodland in eastern Angola.

To the north-east of the range of *B. m. puella*, in the interior of Kenya, in vegetation type 16, the undifferentiated moist type of woodland, populations occur which are heavily suffused with black on the upper parts, but they differ fom the equally dark *B. m. pintoi* in their smaller size. To these populations I append the name *B. m. mystica*.

The subspecies of *Batis molitor* are

Batis molitor molitor (Hahn & Küster)

Muscicapa molitor Hahn & Küster, Vögel aus Asien, Afrika, Amerika und Neuholland (20): pl. 2, 1850: Baviaan's River, Bedford district, Cape Province.

Diagnosis: Males have the head top and the mantle a dark leaden grey with no metallic gloss, the black on the wing coverts and the adjacent mantle is well developed.

Females have the head top and the mantle likewise a dark leaden grey, but not as dark as in the male. The development of black on the mantle adjacent to the wing coverts is somewhat variable, and is usually not particularly well developed and in some instances the black is entirely absent. The colouration of the breast band and the chin spot is variable, from pale to dark. Measurements: $94 \circlearrowleft \text{wing } 55.5 - 66.5 \text{ } (61.97)$, tail 41.0 - 51.5 (46.86), culmen 14.5 - 18.0 (16.10) mm. $68 \circlearrowleft \text{wing } 54.0 - 66.0 \text{ } (60.84)$, tail 41.5 - 52.5 (46.71), culmen 14.5 - 17.0 (15.57) mm.

Material: 260 specimens examined. (Cape Province 105, Natal 57, Moçambique 67, Swaziland 26, Transvaal 5).

Range: The eastern Cape Province from the Sundays River to the Transkei, Natal and Zululand, Moçambique south of the Limpopo River to eastern Swaziland and the extreme eastern Transvaal. Inhabits relatively moist undifferentiated woodland.

Batis molitor palliditergum Clancey

Batis molitor palliditergum Clancey, Ostrich 26 (1): 28, 1955: Sand River, east of Newington, eastern Transvaal.

Diagnosis: The males have the head top and the mantle a paler, more ashen-grey, than in

the nominate race. The colouration of the head top is somewhat variable, but usually paler than in the nominate race. Black colouration is virtually absent from the sides of the mantle.

Females have the head top and the mantle a pale ashen grey, usually paler than that in the males. There is virtually no black on the sides of the mantle. The colouration of the breast band is variable and is not a constant character.

Measurements: $166 \circlearrowleft \circlearrowleft \text{ wing } 56.0 - 71.0 \ (62.02)$, tail $40.5 - 50.0 \ (45.09)$, culmen $14.0 - 18.0 \ (15.9)$ mm. $119 \circlearrowleft \circlearrowleft \text{ wing } 55.0 - 67.0 \ (60.94)$, tail $40.0 - 49.0 \ (44.71)$, culmen $13.5 - 17.0 \ (15.38)$ mm.

Material: 611 specimens examined (Swaziland 6, Transvaal 102, Zimbabwe 329, Zambia 70, Botswana 28, South West Africa 23, Angola 20, Moçambique 19, Malawi 14).

Range: Ranges from eastern Swaziland, the Transvaal and extreme northern Orange Free State, Zimbabwe and the adjacent western Moçambique, eastern and northern Botswana, north-eastern South West Africa and south-eastern Angola, to southern and south-eastern Zambia and adjacent Malawi and the middle Zambesi River valley in Moçambique. Inhabits undifferentiated dry types of woodland in southern Africa, *Brachystegia* and *Julbernardia* woodland and *Colophospermum mopane* woodland.

Batis molitor pintoi Lawson

Batis molitor pintoi Lawson, Bulletin of the British Ornithologists' Club 86 (7): 124, 1966: Fazenda do Cuito, Angola.

Diagnosis: In the males the head top and the mantle are a dark grey, only slightly darker than in the nominate race, but considerably darker than in *palliditergum* and *puella*. The head top is also suffused with metallic blue-black and the breast band is also greener, not blue-black as in *molitor*, *palliditergum* and *puella*. They also average somewhat larger in size of the wing and the tail than these three subspecies.

In the females the head top and the mantle are a darker grey than in the nominate race, palliditergum and puella. There is no gloss on the mantle or the head top. The mantle is more heavily suffused with black than in the other three races and pintoi averages somewhat larger in size of the wing.

In general appearance both the males and the females are considerably blacker on the upper parts than any of the subspecies adjacent to them, but they resemble *mystica* in this respect. Measurements: $37 \circlearrowleft \circlearrowleft \text{wing } 61.0 - 69.0 (65.24)$, tail 41.0 - 47.0 (44.28), culmen 15.0 - 17.0 (15.69) mm. $23 \circlearrowleft \circlearrowleft \text{wing } 58.0 - 67.5 (64.06)$, tail 41.5 - 46.5 (44.09), culmen 14.5 - 17.0 (15.24) mm.

Material: 85 specimens examined (Angola 75, Zambia 10).

Range: Angola, except in the extreme south and north-east, and in extreme north-western Zambia. Inhabits the relatively moist undifferentiated woodland of western Angola and the *Brachystegia* woodlands in the rest of its range in Angola and Zambia.

Batis molitor puella Reichenow

Batis puella Reichenow, Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 10 (1): 125, 1893: Bussissi, southern shore of Lake Victoria.

Batis molitor montana Sjöstedt, Wissenschaftliche Ergebnisse der Schwedischen zoologischen Expedition nach dem Kilimandjaro, dem Meru . . . 1 (3): 109, 1910: Kilimanjaro, Tanzania.

Batis molitor taruensis van Someren, Bulletin of the British Ornithologists' Club 41: 103, 1921: Maungu, south-eastern Kenya.

Diagnosis: Males resemble somewhat *B. m. molitor*, but differ from that taxon in having the mantle more heavily suffused with glossy blue-black. The breast band is glossy blue-black, not green-black as in *pintoi*, from which it also differs in having rather less suffusion of black on the mantle. The head top is generally only very slightly glossy.

Females have the head top and the mantle a blackish grey, not leaden grey as in nominate *molitor*, nor ashen grey as in *palliditergum* and paler than *pintoi*. The mantle is suffused with black, though chiefly in areas adjacent to the wing coverts, but not as heavily as in *pintoi*.

Measurements: 23 ♂ ♂ wing 60.0 — 66.0 (62.50), tail 40.0 — 46.5 (43.00), culmen 14.5 — 17.0 (15.68) mm. 25 ♀ ♀ wing 58.0 — 64.5 (61.02), tail 40.0 — 45.0 (42.48), culmen 14.0 — 16.0 (14.90) mm.

Material: 77 specimens examined (Zambia 26, Angola 4, Tanzania 10, Kenya 34, Uganda 3). Range: Northern Zambia (north-eastern and north-western), extreme north-eastern Angola, western and central Tanzania, merging with *mystica* in southern Kenya, and in western Uganda, extreme southern Sudan, the southern and western Zaire and the Congo Republic. Inhabits *Brachystegia* woodland and relatively moist undifferentiated woodland.

Batis molitor mystica Neumann

Batis mystica Neumann, Journal für Ornithologie 55: 594, 1907; Kikumbuliu, Ukamba, Kenya.

Diagnosis: In the males the head top and the mantle are a dark grey, darker than in any other race of *B. molitor* and very heavily suffused with glossy blue-black, resulting in the upper parts appearing very dark and glossy.

The females have the head top a very dark grey, seldom glossy, though the mantle is similar

to that of the males in having a heavy suffusion of glossy blue-black.

Measurements: 18 $\circ \circ$ wing 56.5 — 65.5 (61.86), tail 40.0 — 46.5 (43.47), culmen 14.5 — 16.5 (15.72) mm. 16 $\circ \circ$ wing 58.5 — 64.0 (60.53), tail 40.5 — 47.0 (43.31), culmen 14.0 — 16.0 (15.12) mm.

Material: 48 specimens examined (Kenya 47, Uganda 1).

Range: A subspecies of the highlands of Kenya and adjacent Uganda. Inhabits the relatively moist undifferentiated woodland of those parts.

Batis soror Reichenow

Batis puella soror Reichenow, Die Vögel Afrikas 2: 485, 1902: Quelimane, northern Moçambique. Batis molitor littoralis Neumann, Journal für Ornithologie 55: 356, 1907: Zanzibar.

Batis soror pallidigula van Someren, Bulletin of the British Ornithologists' Club 41: 103, 1921: Lumbo, Moçambique.

The populations here assigned to *Batis soror* have been the subject of differing opinions and controversy over the years. The controversy has principally revolved around whether these populations be given distinct specific rank, or else subordinated as merely subspecies of *B. molitor*. Reichenow (1902) regarded these populations as *B. puella soror*, *puella* is now regarded as a subspecies of *B. molitor*. Sclater (1930), Vincent (1934), Friedmann (1937), Mackworth-Praed & Grant (1940, 1955, 1963), Peter & Loveridge (1942), Lamm (1953), Winterbottom (1962) and Clancey (1966) regarded *soror* as a subspecies of *B. molitor*. However van Someren (1932), Roberts (1936, 1940), Moreau (1940), White (1963), Rand (1963), Smithers, Irwin & Paterson (1957), Irwin (1962), Lawson (1963, 1966) and Clancey (1969, 1971 & 1980) regarded *soror* as a distinct species.

Lamm (1953) reported supposed intergrades between *soror* and *B. molitor*. Like Irwin (1962) I have examined the same material as did Lamm and agree with Irwin that the specimens do not represent intergrades between *B. molitor* and *B. soror*. Generally speaking the Limpopo River in Moçambique acts as the boundary between *B. molitor* in the south and *B. soror* in the north. Males of *B. soror* and *B. molitor* are not easily separated on colouration and an indifferently prepared study specimen is almost impossible to assign correctly if its measurements are intermediate.

The area of meeting of *B. soror* and *B. molitor* in the south of *B. soror*'s range is in the Limpopo River area. This river valley in the south must represent a formidable barrier to some birds, as the valley near the coast at Joao Belo is 12 km wide. The entire area is very low-lying and consists of swamps and reed beds, originally with no trees whatsoever. However native cultivation in this low-lying area has resulted in the draining of considerable areas as well as the planting of trees, chiefly exotics such as the cashew nut *Anacardium occidentale*, which in some areas in southern Moçam-

bique, where native cultivation has eliminated the indigenous vegetation, reaches the status of the only tree species occurring. To the south of the Limpopo River I have found *B. molitor* in any association of open woodland, not venturing into the forests where *B. fratrum* occurs. The treeveld immediately to the south of the Limpopo River is of a mixed type with a few *Acacias* and many species of *Combretum*, *Gardenia*, *Terminalia*, *Afzelia*, *Kigelia* etc. North of the Limpopo River *B. soror* is to be found in *Brachystegia* woodland and from my observations made at many localities in this southern part of Moçambique it would appear that *B. soror* definitely prefers the more closed type of *Brachystegia* woodland, the mature stands, in preference to the open savanna treeveld areas produced by the effects of native cultivation. It seems probable therefore that *B. molitor* and *B. soror* are not only separated from one another in the south by their habitat preference, but are also geographically separated as well.

I have examined no specimens from the northern part of the range of *B. soror*, nor from the western portions of its range, which I would regard as being intermediate between any of the *Batis* species with which it comes into contact, namely *B. perkeo*, *B. minor* and *B. molitor*. *B. soror* is rather similar to *B. minor suahelicus* in size, differing only in plumage colouration. This particular subspecies of *B. minor* is very small compared to the other subspecies of *B. minor*, which is likewise only responding to its environment and its smallness in size need not be attributed to any gene flow between the populations of *B. minor suahelicus* and *B. soror*, or for that matter with *B. perkeo*. The populations of *B. molitor* in southern Kenya and north-eastern Tanzania are also smaller in size than the populations further inland, and approach *B. soror* in size.

A critical examination of the geographical variation within *B. soror* reveals that minor differences exist, as pointed out by Irwin (1962), but these differences are not geographically delimited or of sufficient magnitude or constancy to permit the subdivision of the populations into subspecies.

Diagnosis: In the males the head top and the mantle are a light grey with an admixture of white on the nape, rump and lower mantle. This admixture of white is more pronounced than in *B. molitor*. The grey of the head top is paler than in *B. molitor* and lacks any blackish suffusion present on the head top in *B. minor* and *B. perkeo*. The lores are white with an extension of white above and past the eye in the form of a white supercilium. *B. molitor* usually has no white supercilium which feature is also rather restricted in *B. perkeo*. The under parts are white with a black breast band which is narrower than in *B. molitor* and *B. perkeo*, but rather similar to that in *B. minor*. The wing and tail are shorter than in *B. molitor*, larger than in *B. perkeo*, but rather similar to *B. minor suahelicus*.

The females are similar to the males but are paler above and the breast band is cinnamon and not black. The chin is also cinnamon but is not in the form of a distinct spot as in *B. molitor*, which species has the breast band russet, which is darker than in *B. soror*. It differs from *B. perkeo* and *B. minor* which species have no chin spot, but the throat is white (with a pale suffusion on the sides of the throat in *B. perkeo*). The lores are white, the supercilium is cinnamon which colour also extends onto the edge of the black mask which passes through the face onto the nape. The wing and the tail are shorter than in *B. molitor* and *B. minor suahelicus*, but larger than in *B. perkeo*.

Measurements: 64 \circlearrowleft \circlearrowleft wing 52.0 — 59.5 (56.20), tail 34.5 — 42.5 (38.77), culmen 14.0 — 16.5 (15.27) mm. 27 \circlearrowleft \circlearrowleft wing 51.0 — 58.0 (54.94), tail 34.0 — 42.0 (38.36), culmen 14.0 — 16.0 (14.87) mm.

Material: 199 specimens examined (Moçambique 138, Zimbabwe 35, Malawi 4, Tanzania 15, Kenya 7).

Range: Moçambique north of the Limpopo River and the low-lying river valleys of immediately adjacent eastern Zimbabwe, the lower Zambesi River valley and the low-lying country of south-eastern Malawi, northwards east of Lake Malawi to eastern Tanzania and coastal south-eastern Kenya. Inhabits *Brachystegia* woodland.

Batis pririt (Viellot)

This is a species of the dry, open treeveld of the semidesertic regions of southern Africa. In the very arid regions it is confined entirely to the few trees lining the dry river and stream beds, whereas in the slightly less arid areas it occurs in the open treeveld associations, which are usually dominated by *Acacia* species.

The males of *B. pririt* have the head top and the mantle a pale grey, rather similar to that of *B. soror*. The lores are white with a thin white supercilium which seldom extends much behind the eye, but it may be absent altogether. The breast band is a glossy black, similar in width to that of *B. molitor*. Males of *B. pririt* are indistinguishable in colouration of the plumage from *B. soror* males.

Females have the head top and the mantle grey, somewhat darker than in the males. The lores are white, the development of the supercilia is rather variable but always thin and seldom extending much behind the eye. The loral spot and the supercilia have an ochraceous suffusion. There is no distinct breast band, the throat, breast and upper flanks are ochraceous, the mid-abdomen and the lower flanks are white.

This species is only satisfactorily distinguished from *B. molitor* on the basis of the colouration of the breast band and the throat in the females.

The populations of *B. pririt* are divided into two subspecies, which, as would be expected from the species continuous distribution, are only moderately well differentiated. They are nevertheless sufficiently distinct to warrant nomenclatural recognition. The subspecies of *B. pririt* are

Batis pririt pririt (Viellot)

Muscicapa pririt Vieillot, Nouveau Dictionnaire d'Histoire Naturelle 21: 486, 1918: Somerset East, eastern Cape Province.

Diagnosis: Males have the head top and the mantle a darker grey than in *affinis*, with a pronounced admixture of black on the mantle. The black facial stripes extend onto the sides of the neck and almost form a complete collar of black, the white on the hind neck being constricted. The white edges to the secondaries are narrow and virtually lacking in some individuals.

The females also have the head top and the mantle a darker grey than *affinis* females, but also have an olivaceous wash. The ochraceous colouration of the breast does not extend round the neck in the form of a collar owing to the black facial stripes' extensions almost obliterating it. Measurements: $46 \circlearrowleft \circlearrowleft$ wing 56.0 - 60.0 (57.66), tail 42.0 - 47.5 (44.28), culmen 14.0 - 16.0 (14.98) mm. $37 \circlearrowleft \circlearrowleft$ wing 54.5 - 58.0 (56.51), tail 42.0 - 46.5 (44.15), culmen 13.5 - 15.5 (14.57) mm.

Material: 135 specimens examined (Cape Province 112, Orange Free State 10, Botswana 13). Range: The Cape Province south of the Orange River, the extreme eastern Northern Cape

The savanna species of *Batis*

Province (Griqualand West) and the western Orange Free State, south-western Transvaal and the south-eastern and central Botswana. Inhabits trees in the subdesert steppe in these areas.

Batis pririt affinis (Wahlberg)

Platystira affinis Wahlberg, Svenska Vetenskaps-Akademien Ofversict af Forhandlingar 1855: 214: Swakop River, Damaraland, South West Africa.

Diagnosis: The males differ from those of the nominate race in being markedly paler above, and in having the head top and mantle a pale grey with no admixture of black on the mantle. The black facial stripes extend onto the neck but do not form a complete collar, the two lobes being separated by the white on the nape. The outer edges of the secondaries are broadly edged with white.

The females have the head top and the mantle a paler grey than in the nominate race, with no admixture of black on the mantle. The deep ochraceous collar is more pronounced and the black facial stripes do not extend to form a collar over the nape.

Measurements: 42 or or wing 55.5 — 61.0 (57.73), tail 41.0 — 46.5 (43.83), culmen 14.0 — 16.5 (15.16) mm. 49 \circ wing 54.0 — 61.5 (56.87), tail 40.0 — 49.0 (44.00), culmen 14.0 — 16.5 (14.95) mm.

Material: 115 specimens examined (Northern Cape Province 21, Botswana 42, South West Africa 51, Angola 1).

Range: South West Africa, except in the extreme north, the north-western Northern Cape Province as far east as Kuruman, and in western Botswana and south-western Angola. Inhabits trees in the subdesert steppe and wooded steppe with abundant *Acacia* and *Commiphora*.

Batis perkeo Neumann

Batis perkeo Neumann, Journal für Ornithologie 55: 352, 1907: Darassam, south-eastern Ethiopia. Batis perkeo is a species of the dry arid thorn scrub, the wooded steppe with abundant Acacia and Commiphora of eastern Africa. Where its range overlaps that of B. molitor and B. soror in Kenya and Tanzania, it is found in a much drier environment. B. perkeo overlaps widely with B. minor, but the habitat requirements of these two species are such that there is ecological separation between them. B. perkeo has a limited marginal overlap in range with B. orientalis which Benson (1946) reported occupy the "same area and environment". If this is so then it would appear that in a restricted area of southern Ethiopia B. orientalis and B. perkeo have similar ecological requirements and may be in direct competition with one another. There must be significant differences in the Specific-Mate Recognition Systems of the two species to provide adequate isolating mechanisms to prevent interspecific hybridisation.

Diagnosis: Males have a white supraloral spot, with a white supercilium only very poorly developed, often reaching to above the eye, but rarely ever beyond it. A white nuchal spot is present. The head top and the mantle are concolourous, being a dark grey. The primaries are narrowly edged on the outer web with white, the secondaries more broadly edged with white on the outer web. Males differ from *B. soror* males in having the head top a darker grey and with an admixture of glossy blue-black in the mantle, which feature is absent in *B. soror*.

Females have the supraloral spot white with a strong rusty tinge, the 'supercilium' seldom extending even as far as the eye. The nuchal spot is present though often not well marked, and is white with a buffy suffusion. There is a slight development of a buffy coloured nuchal band. The head top and the mantle are concolourous, being grey. The primaries are narrowly edged on the outer web with white, the secondaries more broadly edged with white on the outer web. The throat is white medially with

the lateral margins pale buffy. The breast band is a pale buff, not deeply saturated in colour.

Both the male and female of *B. perkeo* are smaller than any other species of *Batis*. In examining *B. perkeo* I can see no geographical variation worthy of use in subdividing the species into subspecies.

Measurements: 25 \circlearrowleft \circlearrowleft wing 48.5 — 55.0 (51.96), tail 30.0 — 37.5 (33.86), culmen 14.0 — 16.5 (15.26) mm. 13 \circlearrowleft \circlearrowleft wing 49.0 — 53.5 (50.69), tail 30.0 — 35.5 (32.73), culmen 13.5 — 15.5 (14.50) mm.

Material: 50 specimens examined. (Tanzania 3, Kenya 38, Uganda 4, Sudan 2, Ethiopia 3)

Range: The interior regions of Somalia and eastern and southern Ethiopia, through the arid regions of northern and eastern Kenya to the arid regions of the extreme northeastern Tanzania. Also extends from southern Ethiopia westwards to the extreme southeastern Sudan and eastern Uganda. Inhabits wooded steppe with abundant *Acacia* and *Commiphora*.

Batis senegalensis (Linnaeus)

This species inhabits the sub-saharan woodland savannas of West Africa, to the north of the tropical lowland forests and south of the Sahara desert. It ranges from Senegal in the west to the Cameroon in the east. The only savanna species with which *B. senegalensis* approaches in range is *B. minor*. I can find no characters on which to validate the name *B. s. togoensis* Neumann: Misahöhe, Togo. Specimens examined from the western part of West Africa appear to be closely similar in colouration and size when compared with those from the eastern portions of the species range.

The characters, range etc of Batis senegalensis are:

Batis senegalensis (Linnaeus)

Muscicapa senegalensis Linnaeus, Systema Naturae 12th ed. 1: 327, 1766: Senegal. Batis senegalensis togoensis Neumann, Journal für Ornithologie 55: 350, 1907: Misahöhe, Togo.

Diagnosis: Males have a white supraloral spot which is very prominent and which extends in the form of a supercilium to the nape as a very broad white stripe which is also a prominent feature of the bird. The nuchal spot is white and is bounded on both sides by the black stripes which extend from the lores, above and below the eye onto the nape. The secondary coverts are brown. The head top and mantle are not concolourous, the head top being a dark, blackish olive brown whereas the grey mantle is heavily suffused with olive-russet. There is virtually no black in the mantle of *B. senegalensis* males. The breast band is black.

Females have the breast band buff, which colour is somewhat intermediate between the colours of the breast band of *B. pririt* and *B. perkeo*, which is very much paler than the chestnut colouration of the breast band of females of *B. molitor*, *B. orientalis* (except *B. o. lynesi*) and *B. minor*. This breast band is rather similar in colouration to that in *B. soror* females. The throat has a suffusion of buff, the same colour as the breast band. This suffusion of buff is uniform and not confined to the lateral surfaces as in *B. perkeo*. The density of the suffusion of buff is somewhat variable and in some specimens examined has been hardly present. The supercilium is well marked and has a marked suffusion of buff. The white edges to the wing coverts are strongly tinted with buff, as is the supraloral spot. The upper parts are olive brown, the head top being slightly darker than the mantle. The nuchal spot is buff.

Material: 20 specimens examined. (Senegal 4, Mali 3, Ivory Coast 1, Ghana 5, Nigeria 2, Cameroon 1, 'Africa' 4.)

Range: West Africa from Senegal eastwards north of the Upper Guinea forests and south of the Sahara desert, to Nigeria and the Cameroon. Inhabits the woodland savannas of these regions.

Batis minor Erlanger

Males have the head top and the mantle dark grey, usually with a heavy suffusion of glossy blue-black, the head top is usually rather darker than the mantle. The supra loral spot is white, the white supercilium is well developed, broad, but rather diffuse and not clearly defined. It extends beyond the eye onto the hind crown, almost reaching the white nuchal spot. In some instances the white supercilium does reach the nuchal spot. The breast band is a glossy blue-black, rather narrow but narrower than in *B. molitor*, rather more like *B. soror* in width. The primaries are only very narrowly edged with white on the outer web, the secondaries are edged narrowly with white on the outer web, the edging being slightly broader than the edging to the primaries.

The females have the head top and the mantle a dark blackish grey, almost black. The supraloral spot is white and extends, as in the male, in the form of a prominent, but diffuse, white supercilium which extends almost onto the nape. The breast band is russet, as in *B. molitor* but is considerably narrower in width than in that species. The throat is white without a coloured chin spot. The colour characteristics of the primaries and the secondaries are similar to those in the males.

The grouping of the various populations of B. minor into formal subspecific categories has resulted in a number of subspecies being proposed. Rand (1963), though only dealing in detail with the eastern populations, admitted no fewer than seven subspecies, namely B. m. minor, B. m. suahelicus Neumann: near Moshi, Tanzania, B. m. erlangeri Neumann, Gara Mulata, near Harar, Ethiopia, B. m. congoensis Neumann: Ngombi, lower Congo, B. m. nyanzae Neumann: Kampala, Uganda, B. m. chadensis Alexander: Arrege, west of Lake Chad and B. m. batesi Bannerman: Bamenda, Cameroon. The populations placed by Rand as B. m. chadensis I place in the species B. orientalis. Rand gives a useful résumé of the variation within the eastern populations of B. minor. Chapin (1953) admitted minor, erlangeri, nyanzae, suahelicus and congoensis, though considering that congoensis was of doubtful status. Friedmann (1937) recognised erlangeri, chadensis, nyanzae and suahelicus, Gyldenstolpe (1924) admitted *nyanzae*, Traylor (1962) also admitted *nyanzae* with which he synonymised congoensis. Schouteden (1954) admitted both nyanzae and congoensis as valid while Friedmann & Loveridge (1937), Stone (1936) and Jackson (1938) recognised *nyanzae* and suahelicus.

Van Someren (1929) admitted *minor*, *suahelicus* and *nyanzae*. Benson (1946) considered *erlangeri* and *nyanzae* to be valid taxa. Bannerman (1936) admitted *congoensis* and *batesi*. Mackworth-Praed & Grant (1940, 1955) admit as the only valid subspecies *minor*, *erlangeri* and *suahelicus*. White (1963) admits only *minor* and *erlangeri* placing *suahelicus* as a synonym of *minor* and *congoensis*, *nyanzae* and *batesi* as synonyms of *erlangeri*.

In this work I propose to admit as valid subspecies of *Batis minor* the following subspecies: *minor* of southern Somalia, *suahelicus* of the eastern lowlands of Kenya and north-eastern Tanzania and *erlangeri* of Ethiopia, Sudan, Uganda, Zaire, Came-

roon to Gabon and the lower Zaire and north-western Angola. I synonymise *congoensis*, *nyanzae* and *batesi* with *erlangeri*.

The populations grouped together as nominate *minor* from southern Somalia are very similar to those populations from eastern Kenya and Tanzania placed as *suahelicus* as regards plumage colouration. Rand (1953) found no colour differences between the Somalia populations and those of eastern Kenya and Tanzania. He admits the latter populations as *suahelicus* on the basis of their larger size. Significant levels of difference do exist between the wing and tail of these two population groupings. It would also appear that the breast band in the females of *suahelicus* is narrower than that in *minor*.

The populations placed as *erlangeri*, that is, all the populations of *B. minor* not placed here in either *minor* or *suahelicus*, are significantly larger in size than those of *minor* and *suahelicus*. On size alone absolute separation can be effected. In addition *erlangeri* has the mantle distinctly darker, a blacker grey, than in the other two subspecies and there is a greater admixture of blue-black in the mantle. The head top though is less glossy blue-black. The females of *erlangeri* have the mantle with a light suffusion of olive and the mantle is clearly more olive-brown in appearance.

B. minor nyanzae has been admitted as valid by many authors. While the colour of the head top is blacker in some specimens than in minor, suahelicus and the erlangeri populations from Ethiopia, the feature is not constant in either the populations referred to nyanzae or the other three groups of populations, and so is unsuitable as a distinguishing feature. The colour of the mantle hardly differs from that of erlangeri from Ethiopia and may have greater admixture of black than suahelicus and minor in the males. In the females the head top does appear to be darker, almost black, when compared with suahelicus, but it is not constantly darker than erlangeri from Ethiopia. The grey of the mantle is lightly suffused with olive. The breast bands of nyanzae and erlangeri from the type localities are similar. I can see no constant feature on which to separate the populations usually classed as nyanzae and erlangeri of Ethiopia. I can similarly find no differences between nyanzae, congoensis and batesi. No size differences exist between these populations.

The range of *B. minor* overlaps the ranges of five of the remaining six species of savanna dwelling *Batis* species, with *B. pririt* being the only savanna species not coming into contact with *B. minor*.

Batis minor ranges from the highlands of Ethiopia, south-eastern Sudan, southern Somalia and north-eastern Tanzania to Uganda, Zaire and northern Angola, the Gabon and Cameroon. The habitat in which B. minor lives differs somewhat in the different parts of its range, which covers a considerable portion of central Africa, with minor in drier ecotypes than suahelicus and erlangeri. While there is a limited amount of sympatry with other species of Batis, Batis minor is nevertheless usually ecologically separated from them.

The males of the savanna species of *Batis* are generally similar to one another, the main distinguishing characters being the colouration of the head top and mantle. Size is also an important consideration in distinguishing between the different species, but in carrying out a comparison it is necessary to compare the populations which are adjacent to one another as considerable differences exist in the different subspecies. The principal differences between the species of savanna *Batis* lie in the females where

not only do colour differences exist but there are also colour pattern differences. The subspecies of *B. minor* are

Batis minor minor Erlanger

Batis orientalis minor Erlanger, Ornithologische Monatsberichte 9: 181, 1901: Juba River, Somalia.

Diagnosis: Males have the head top and mantle a dark slate grey with no admixture of glossy blue-black on the head top, but there is some glossy blue-black on the mantle. The supraloral spot is white and this extends over the eye as a prominent white supercilium.

Females have the head top and mantle dark slate grey, and have a broad chestnut breast band. Measurements: $4 \circlearrowleft \circlearrowleft \text{wing } 54.0 - 56.0 (55.25)$, tail 34.5 - 39.0 (36.25), culmen 15.0 - 15.5 (15.17) mm. $5 \circlearrowleft \circlearrowleft \text{wing } 52.0 - 53.0 (52.50)$, tail 34.0 - 36.5 (35.50), culmen 14.0 - 15.5 (14.80) mm.

Material: 10 specimens examined (Somalia 10).

Range: Only in southern Somalia, in wooded steppe with abundant Acacia and Commiphora.

Batis minor suahelicus Neumann

Batis minor suahelicus Neumann, Journal für Ornithologie 55: 353: 1907: near Moshi, Tanzania.

Diagnosis: The males are rather similar to those of the nominate subspecies in colouration but they average somewhat larger in size of the wing and tail.

The females are likewise similar to those of the nominate subspecies in colouration but they average larger in size of the wing and tail. The breast band is narrower than that in females of the nominate subspecies.

Measurements: $24 \circ \circ$ wing 54.0 - 59.0 (56.75), tail 36.0 - 41.5 (38.52), culmen 15.0 - 16.5 (15.82) mm. $28 \circ \circ$ wing 53.0 - 59.0 (56.41), tail 36.5 - 43.0 (39.35), culmen 14.5 - 16.0 (15.43) mm.

Material: 54 specimens examined. (Tanzania 13, Kenya 41).

Range: South-eastern Kenya as far east as Endau Mt. and Kibwezi to north-eastern Tanzania as far east as Kilimanjaro Mt. and Kilosa district and south as far as the Kilwa district. Inhabits wooded steppe with abundant *Acacia* and *Commiphora* but in the south in moist undifferentiated woodland.

Batis minor erlangeri Neumann

Batis minor erlangeri Neumann, Journal für Ornithologie 55: 353, 1907: Gara Mulata, near Harar, Ethiopia.

Batis minor congoensis Neumann, Journal für Ornithologie 55: 354, 1907: Ngombi, lower Congo, Zaire. Batis minor nyanzae Neumann, Journal für Ornithologie 55: 354, 1907: Kampala, Uganda.

Batis bella batesi Bannermann, Bulletin of the British Ornithologists' Club 44: 4, 1923: Bamenda, Cameroon.

Diagnosis: The males are larger in size of wing and tail than *minor* and *suahelicus*. The mantle is a distinctly darker, blacker, grey than in *suahelicus* and there is a greater admixture of blue-black in the mantle. The head top is less glossy blue-black than in the other two races.

Females are likewise larger in size of the wing and tail than *minor* and *suahelicus*. The mantle has a suffusion of olive and appears more olive brown than in the other two subspecies. Measurements: $66 \circ \circ$ wing 57.0 - 67.5 (61.80), tail 38.0 - 51.0 (44.25), culmen 14.0 - 17.5 (16.50) mm. $49 \circ \circ$ wing 57.0 - 64.5 (60.98), tail 40.0 - 50.0 (44.14), culmen 15.0 - 17.5 (15.98) mm.

Material: 134 specimens examined. (Angola 8, Zaire 17, Congo Republic 2, Gabon 1, Cameroon 15, Central African Republic 3, Uganda 27, Kenya 5, Sudan 27, Ethiopia 29).

Range: The highland country of Ethiopia, the rift valley and south western Ethiopia, the south-western Sudan, western Kenya, Uganda and Uelle districts of Zaire, Central African Republic westwards to Cameroon and the Cameroon/Nigeria border, south to the Gabon, the Congo Republic and southern Congo and northern Angola. Does not inhabit the great Congo low-land forests, north and south of which it inhabits the moist savanna-forest mosiac woodland

and the moist *Isoberlinia* woodland north of the lowland forests and the forest-savanna mosiac woodland. To the east and north-east of the lowland forests in Uganda it inhabits the moist undifferentiated woodland steppe, from whence it extends north-east across the southern Sudan to Ethiopia in the relatively dry woodlands.

Batis orientalis (Heuglin)

Males of *B. orientalis* have the head top and the mantle grey, not glossy blue-black. The supraloral spot is white and a white supercilium extends from the supraloral spot past the eye to reach the nuchal spot.

Females have the head top and the mantle grey and have a russet breast band and a white throat with no russet colouration on the throat.

B. orientalis ranges from El Obeid in the northern Sudan, south-eastwards along the Red Sea to the extreme eastern Somalia and south through the eastern Sudan to the southern Sudan and Tchad and extreme north-eastern Nigeria in the region of Lake Tchad, through Ethiopia to the extreme northern areas of Kenya. This species is generally in rather dry woodland savanna country at a lower elevation than B. minor.

Geographical variation in the populations of *Batis orientalis* is reflected in size differences and also colour differences of the plumage. Nominate B. orientalis is considerably larger in wing and tail measurements than other subspecies of *B. orientalis*. The males have the head top and the mantle a dark blackish grey, the females also have the head top and the mantle a dark grey. With the exception of Friedmann (1937) most authors, for example Mackworth-Praed & Grant (1940, 1955) and White (1963) place the populations I here place as B. o. bella as synonymous with the nominate race. The populations I place as bella are considerably smaller than the nominate race, the males have the head top and the mantle paler grey than in the nominate subspecies. The females likewise have the mantle a paler grey suffused with olive. Friedmann (1937) gives the range of nominate B. orientalis as 'Eritrea, Bogosland, south to the western part of the Hawash Valley and into northern Shoa', and bella as 'northern Somaliland, the eastern part of the Hawash Valley, south to eastern Arussi-Gallaland and Gurraland to the northern part of Italian Somaliland'. As there are clear-cut colour differences between the populations I have placed as orientalis and bella and that it would appear as if there are also significant differences in the sizes of these two subspecies, I keep them distinct from one another.

I can find no evidence to support the validity of the name *B. o. somaliensis* Neumann: Denek River, Somalia, which name must be placed in the synonymy of *bella*.

In the Red Sea Province of the Sudan, populations of *B. orientalis* occur which can be distinguished from the neighbouring populations of *B. o. orientalis* and *B. o. bella*. Females of the populations of this region differ from the females in the other populations in having a paler, more yellowish breast band. To these populations the name *B. o. lynesi* Grant & Mackworth-Praed: Sinkat, Sudan, can be applied. Insufficient material was available for measurement to enable any reliable conclusions to be drawn from the size of the wings and the tails of the members of *lynesi*. It would appear that the populations assigned to *lynesi* may be smaller than those of the nominate race, but rather similar in size to the other subspecies of *B. orientalis*.

The populations placed as B. o. chadensis Alexander: Arrege, west of Lake Tchad, range from the western and southern Sudan westwards to the Lake Tchad area of

extreme north-eastern Nigeria. *B. o. chadensis* males are virtually indistinguishable from those of the nominate race on plumage colouration, but are darker than *B. o. bella. B. o. chadensis* males are however smaller than those of the nominate race. The females of *chadensis* have the breast band narrower than that in the other subspecies of *B. orientalis* and the head top and the mantle are washed with brown. The remiges are brown and not black and the white supercilium is prominent and well developed. *B. o. chadensis* females are smaller than those of the nominate race.

The ranges, characters etc. of the subspecies of B. orientalis are as follows.

Batis orientalis orientalis (Heuglin)

Platystira orientalis Heuglin, Ornithologie Nordost-Afrikas 1: 449, 1871: Modat Valley, Ethiopia.

Diagnosis: The males have the head top and the mantle a dark blackish grey, and the females similarly have the head top and mantle a dark grey. A large sized subspecies.

Measurements: $2 \circ \circ$ wing 63.5 - 64.5 (64.0), tail 48.0 - 48.5 (48.25), culmen 16.5 mm. $2 \circ \circ$ wing 60.5 - 61.5 (61.0), tail 45.0, culmen 16.0 mm.

Material: 8 specimens examined. (Ethiopia 8).

Range: In Ethiopia, from Eritrea, Bogosland, south to the western part of the Hawash River valley and into northern Shoa. Occurs in very arid *Acacia* scrub.

Batis orientalis bella (Elliot)

Pachyprora bella Elliot, Field Museum Publications in Ornithology 1897: 47, 1897: Hullier, Somalia. Batis orientalis somaliensis Neumann, Journal für Ornithologie 55: 351, 1907: Denek River, Somalia.

Diagnosis: The males have the head top and the mantle a paler grey than in the nominate race. The size of the wing and tail are considerably smaller than in the nominate race.

Females have the head top and the mantle a paler grey than in the nominate race and the mantle is suffused with olive. The wing and tail are smaller than in *orientalis*.

Measurements: $30 \, \circ \circ \, \text{wing } 56.0 - 60.0 \, (57.88)$, tail $37.0 - 45.5 \, (40.36)$, culmen 14.0 $- 17.0 \, (15.29) \, \text{mm}$. $22 \, \circ \circ \, \text{wing } 55.0 - 60.0 \, (56.77)$, tail $36.5 - 41.5 \, (39.98)$, culmen 14.0 $- 15.5 \, (14.96) \, \text{mm}$.

Material: 72 specimens examined. (Somalia 33, Ethiopia 37, Kenya 2).

Range: Eastern Ethiopia and northern Somalia, southern Ethiopia and extreme northern Kenya and south-eastern Sudan. Occurs in dry *Acacia* woodland.

Batis orientalis chadensis Alexander

Batis chadensis Alexander, Bulletin of the British Ornithologists' Club 21: 1908: Arrege, west of Lake Tchad.

Diagnosis: Males are virtually indistinguishable from males of the nominate race in respect of the darkness of the head top and mantle, but are paler than *B. o. bella*. The size of the wing and the tail are smaller than in the nominate race.

Females have the breast band narrower than in the other races of *B. orientalis* and the head top and the mantle are washed with brown. The remiges are brown, not black. The white supercilium is very well developed and is a prominent feature of this bird.

Measurements: 11 $\circ \circ$ wing 56.0 — 62.0 (58.23), tail 38.0 — 43.0 (39.95), culmen 15.0 — 17.0 (16.33) mm. 14 $\circ \circ$ wing 55.5 — 59.5 (57.28), tail 38.5 — 43.5 (41.31), culmen 16.0 mm. Material: 34 specimens examined. (Tchad 4, Sudan 25, Central African Republic 2, Ethiopia 1, Uganda 1, Nigeria 1).

Range: Extreme western Ethiopia, Sudan westwards to Lake Tchad and extreme north-eastern Nigeria, and northern Uganda and the Central African Republic. Occurs in dry *Acacia* woodland to subdesert steppe.

Batis orientalis lynesi Grant & Mackworth-Praed

Batis orientalis lynesi Grant & Mackworth-Praed, Bulletin of the British Ornithologists' Club 60: 92, 1940: Sinkat, Sudan.

Diagnosis: Differs from the other subspecies of B. orientalis in that the female has a paler, more yellowish, breast band.

Measurements: $2 \circlearrowleft \circlearrowleft$ wing 56.5 - 57.5 (56.75), tail 38.0 - 41.0 (39.50), culmen 15.0 mm. $1 \circlearrowleft$ wing 59.0, tail 41.0, culmen 15.0 mm.

Material: 3 specimens examined. (Sudan 3).

Range: Confined to the Red Sea Province of the Sudan. Occurs in subdesert steppe.

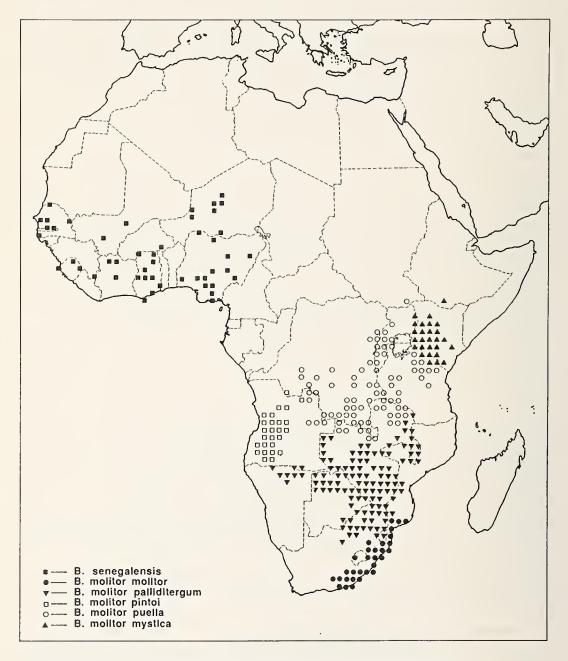


Fig. 3: Ranges of populations of Batis molitor and Batis senegalensis.

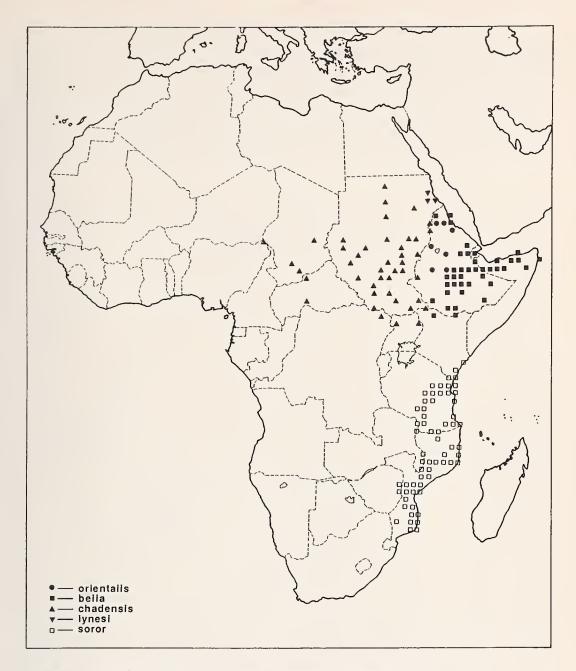


Fig. 4: Ranges of populations of Batis orientalis and Batis soror.

Comments on the evolutionary history of the savanna species of Batis

The modern genera of many small African passerine birds could possibly have originated during the Quaternary period (contra Sibley & Ahlquist 1985) and it is the climatic changes during this period that played an important role in altering the vegetation patterns in Africa and provided the stimulus for the evolution of many species. No work on the Quaternary changes in climate, flora and fauna would be complete without reference to Moreau's (1966) and Hamilton's (1982) work on the subject.

During the past one million years the earth has experienced a number of climatic changes resulting in glacial episodes during which the temperatures were considerably lower than at present and rainfall was markedly less than under present conditions. Major glacial periods were separated by periods during which the temperatures rose again and the rainfall also rose to levels above those of the present. These interglacial periods were interspersed with minor glacial or colder, drier periods. The last major glaciation which affected Africa had its peak at about 18,000 years Before Present.

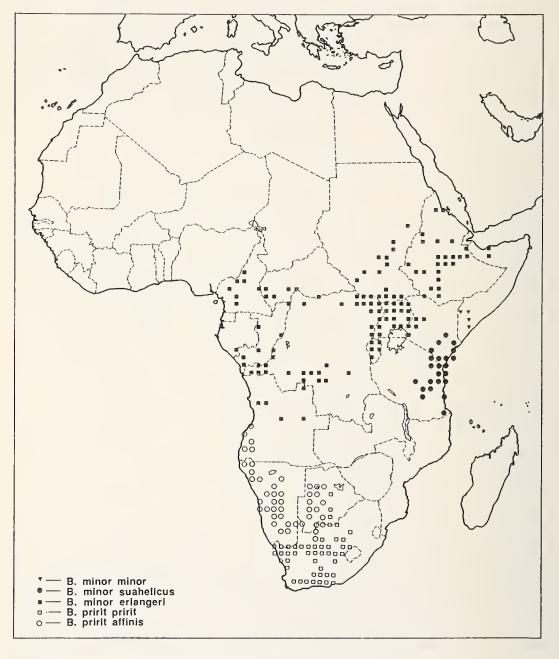


Fig. 5: Ranges of populations of Batis minor and Batis pririt.

The savanna species of Batis

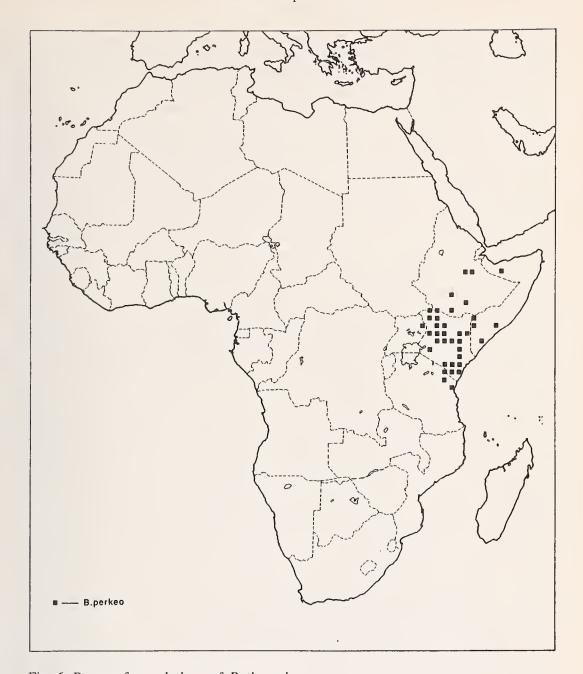


Fig. 6: Range of populations of Batis perkeo.

It has been reasonably well substantiated that a correlation exists between the glacial episodes in various parts of the world. Large ice sheets covered parts of the northern hemisphere during the last major glacial at 18,000 B. P. Ice sheets were not formed on the African continent though there were substantial enlargements of the glaciers on many of the high mountains in Africa.

A drop in temperature and decreased precipitation would have had wide ranging effects on the vegetation of Africa. The forests which are so dependent on precipitation, often well spaced during the year would have suffered and would have demini-

shed to small refugia. During the interglacial periods with increased temperatures and rainfall the montane forests and their associated faunal communities would have descended to lower altitudinal levels than under present conditions. The lowland forests would likewise have extended the areas occupied by them. This expansion of the forests would have enabled the forest species of birds to expand their ranges considerably.

The expansion of the forest zones would have caused a shift in the other vegetational zones, the major one concerning the genus *Batis* being the woodland savannas, when the savanna blocks would have been fragmented. Some consideration of the evolution of the forest species of *Batis* has been given by Lawson (1986). While the glacial periods were responsible for the isolation of the populations of forest haunting species of *Batis*, it was the interglacial periods that were responsible for the evolution through isolation of the savanna species of *Batis*. The extent of differentiation of the populations isolated in their forest or savanna refugia could well have depended on the size of the isolated block of forest or savanna. The smaller the size of the isolated population the more rapid could have been the differentiation.

During the interglacial which preceded the glacial maximum of some 18,000 B. P. the savannas of Africa were fragmented by the expansions of the forests and the considerable extensions in the surface areas of the lakes. The savannas persisted in areas where local climatic conditions and elevation were such as to prevent the development of forests. They acted not only as reservoirs for the savanna populations of *Batis*, but as incubators for the species to come.

In the south-western and western parts of southern Africa a desert exists at present with a considerable semi-arid savanna belt on the periphery. These areas have considerable antiquity and at best would have had a moister type of treeveld savanna than at present, with a desert persisting due to local conditions. The populations of the savanna *Batis* which were isolated in this area attained through isolation specific status and presently bear the name *B. pririt*. It seems probable that the populations which gave rise to *B. molitor* must also have been isolated in the central parts of southern and central Africa, in the moister types of savanna which persisted in Zimbabwe, Zambia and Angola.

B. soror originated from populations sandwiched between Lake Malawi, the mountain chain sweeping from the northern Lake Malawi to north-eastern Tanzania, all of which had forests descending to lower levels which may have been continuous, and the Indian Ocean. Much of the area at present occupied by B. soror along the low coastal plains of eastern Africa would have been covered in lowland forest during the interpluvial period. B. pririt, B. molitor and B. soror all have males which are remarkably similar to one another. Differentiation has occurred principally in the females. B. soror is smaller than B. molitor in response to its low altitude range and its warmer environment.

The next group of populations to consider were those which showed a tendency to the loss of the buffy chin-spot in the females. They may well have been isolated from the more southerly populations at an earlier time which would have allowed a more pronounced development of the tendency to lose the chin spot. They were probably separated at an earlier time from these southerly populations than these populations were from one another. This may have been due to the effective barrier offered at an early stage of the development of the interpluvial period by the belt

of highland country with montane forest from the northern end of Lake Malawi to north-eastern Tanzania, and the enlarged coastal lowland forests in eastern Africa. These more northerly populations were in turn isolated in patches of savanna with the prolongation of the interglacial period.

The populations now placed as *B. minor* may well have been isolated in moister treeveld savanna to the north of Lake Victoria. In *B. minor* the females lost the buffy chin-spot and both sexes developed darker head-tops and mantles in response to the moister conditions in which they lived.

Somalia, north-eastern Kenya and south-eastern Ethiopia have long been a very arid, desertic region. The populations in this area are small bodied in response to this warm, low-lying area. The females have all but lost the buffy throat patch. These populations are *B. perkeo*.

B. orientalis is a pale headed, pale mantled species in which the females, like B. minor, have totally lost the chin spot. This species was isolated in the dry treeveld savannas of north-central and north-eastern Africa, where such treeveld would have persisted under interglacial conditions. During the interglacial Lake Chad expanded about 500 kms north and also considerably further south than its present limits, reaching to the edge of the Cameroon highlands in the south and almost to Tibesti in the north. This Megachad would have provided a most effective barrier against movements of birds east and west of this area. B. orientalis originated to the east of the barrier, and B. senegalensis originated west of this barrier in similar dry treeveld savanna. B. senegalensis was the only savanna species to evolve west of Megachad as the savanna in this area was continuous and not further subdivided.

An examination of the figures derived from the mathematical analyses is of interest. Figure 1 represents the three-dimensional plot derived from the multi-dimensional scaling and Figure 2 the dendrogram derived from the U.P.G.M.A. method. All the B. molitor subspecies are clustered together and are derived from the same branch that gave rise to B. soror and B. pririt. This was considered to be the case with these three species. The B. minor/B. orientalis cluster of subspecies cluster well but the dendrogram aligns B. orientalis orientalis and B. minor erlangeri together. This complex of B. minor and B. orientalis populations is perplexing as the two are essentially separated on the darkness of the upper-parts. It is not impossible that this may be erroneous and that more than two species may be involved in this complex of species. Some of the populations are very poorly known in the field and until such time as field studies of these B. minor/B. orientalis populations are undertaken some doubt must be entertained as to their true relationships. The dendrogram may well be shown to be correct. In the analyses of the savanna populations, and the forest populations given in Lawson (1986), this B. orientalis orientalis/B. minor erlangeri cluster is the only one which does not fit the supposed relationships of the *Batis* populations based on non-mathematical considerations. Both B. senegalensis and B. perkeo show early separation from the savanna Batis stock, suggesting longer periods of separation and isolation or smaller populations during isolation for diversity to develop. The results of the mathematical analyses, with one exception, closely mirror the hypothesised relationships between the populations of savanna dwelling Batis.

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